

Prey Search Behavior of the Imperial Cormorant (*Phalacrocorax atriceps*) during the Breeding Season at Punta León, Argentina

Author(s): Sabrina Harris, Flavio Quintana and Andrea Raya Rey

Source: Waterbirds, 35(2):312-323. 2012.

Published By: The Waterbird Society

URL: <http://www.bioone.org/doi/full/10.1675/063.035.0212>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

Prey Search Behavior of the Imperial Cormorant (*Phalacrocorax atriceps*) during the Breeding Season at Punta León, Argentina

SABRINA HARRIS^{1,*}, FLAVIO QUINTANA^{1,2} AND ANDREA RAYA REY³

¹Centro Nacional Patagónico, CENPAT-CONICET, Bvd. Brown 2915, U9120ACD Puerto Madryn, Chubut, Argentina

²Wildlife Conservation Society, Amenábar 1595, C1426AKC Ciudad de Buenos Aires, Argentina

³Centro Austral de Investigaciones Científicas, CADIC-CONICET, Bernardo Houssay 200, V9410CAB Ushuaia, Tierra del Fuego, Argentina

*Corresponding author; E-mail: harris@cenpat.edu.ar

Abstract.—Behavior by a foraging seabird during the breeding season can be examined by analyzing time invested throughout the foraging route to determine the presence of Area-Restricted Search (ARS) as well as other characteristics related to the shape of the foraging path and activity (flying, resting or diving). Forty-six Imperial Cormorants (*Phalacrocorax atriceps*), 18 males and 28 females breeding at Punta León, Argentina (43°04'S; 64°2'W), were fitted with GPS loggers recording one foraging trip (sampling interval: 1 second) in 2004, 2005, 2007 and 2008. Trip duration was longer, on average, for females (6.3 ± 1.9 h) than males (5.3 ± 1.6 h) (Mann-Whitney U test $z = 1.45$, $P = 0.026$), but year had no significant effect on any of the path characteristics. ARS was detected in 43 individuals, 22 of which made smaller-scaled searches nested within larger ARS areas. Search scale was not correlated to maximum distance reached and did not differ between sexes nor years. Cluster analysis separated four types of behavior: short direct return trips ($N = 7$), long direct return trips ($N = 31$), random flight searches ($N = 6$) and loops ($N = 2$), with each behavioral type present in both sexes. Behavioral variability within a population may be due to differences in targeted prey type and spatio-temporal stability during the season, as well as to individual physiological constraints and life-history traits linked to how individuals search for food at sea. Received 8 June 2011, accepted 28 October 2011.

Key words.—Area-Restricted Search, Imperial Cormorant, *Phalacrocorax atriceps*, search behavior.

Waterbirds 35(2): 312-323, 2012

Seabirds must find prey in a highly heterogeneous and dynamic oceanic environment (Orians and Pearson 1979; Fauchald *et al.* 2000; Pinaud and Weimerskirch 2007). In order to do so, marine predators possess physical (White *et al.* 2008), physiological (Angelier *et al.* 2007) and/or behavioral traits (Davoren *et al.* 2003; Pinaud and Weimerskirch 2005; Weimerskirch *et al.* 2007) that maximize their probability of prey acquisition and, ultimately, impact positively on their fitness (Charnov 1976).

Predators searching for prey that is distributed in patches can perform a Correlated Random Walk (CRW) (Kareiva and Shigesada 1983), which is represented by a sum of straight movements of random length with a given degree of correlation between each move. CRWs are effective when a predator's perceptual range is small (Zollner and Lima 1999) or when prey systems are unpredictable or unstable in space and time (Hawkes 2009). However, if the predator has additional information regarding the location of prey patches, such as through perceived navigational cues or local enhancement (Davoren

et al. 2003; Fauchald 2009), and/or is able to learn from previous experience, oriented and memory-based movements may be developed (Mueller and Fagan 2008). Among oriented behaviors, Area-Restricted Search (ARS) (Kareiva and Odell 1987) is one that involves an increase in time invested in certain areas of the foraging path (Fauchald and Tveraa 2003). An increase in search effort triggered by prey detection, either directly or by its correlation with oceanographic variation, has been described for both large-scale marine foragers such as albatrosses and petrels (Fritz *et al.* 2003; Suryan *et al.* 2006; Pinaud and Weimerskirch 2007), and small-to medium-scale foragers such as Northern Gannets (*Morus bassanus*), Guanay Cormorants (*Phalacrocorax bougainvillii*) and boobies (*Sula* sp.) (Hamer *et al.* 2009; Weimerskirch *et al.* 2009; Zavalaga *et al.* 2010).

Prey distribution at-sea may be predictably linked to environmental variables such as sea temperature (Pájaro *et al.* 2005), depth range (Fernández *et al.* 2007), local substrate and/or its own food source (Pájaro 2002). Seabirds may begin searching

at a larger scale, tracking environmental cues of prey presence, followed by a smaller-scale search to home in on prey using a strategy termed nested Area-Restricted Search (Fauchald and Tveraa 2006). Individuals that search at more than one scale may be detecting different variables at each scale (as in Paiva *et al.* 2010) and even use more than one mechanism to search for prey, such as olfaction in procellariiforms (Nevitt 1999), or vision in species that rely mostly on sight above and below water for foraging (White *et al.* 2008). Within a stable environment a benthic prey that is not visible to a seabird searching while in flight may be subject to this kind of behavior.

A given foraging trip is the outcome of a predator-prey interaction within an ecological and temporal context (Perry and Pianka 1997; Fauchald 2009) and will depend on the ability of the predator to track prey, or environmental characteristics indicating prey presence, that may remain relatively stationary or change with time (e.g. daily or seasonal migrations of pelagic fish (Pájaro 2002)). If prey distribution varies from one breeding season to the next, foraging behavior by individuals from a given colony may also differ between years (Quillfeldt *et al.* 2011). Sinuosity of a predator foraging track may respond to prey abundance, and/or distribution, as well as to satiation (Zoller and Lima 1999), with individuals moving in straighter paths when prey is scarce or when their energetic levels are low. Segregation of search areas, time of day of foraging and depth exploitation according to sex has been detected for various species of seabirds (Lewis *et al.* 2002; Quintana *et al.* 2011, among others). Age can also influence foraging behavior, as inexperienced individuals of a given species are sometimes less efficient foragers than older individuals (Daunt *et al.* 2007). Further, interactions with conspecifics at-sea may influence an individual's foraging decisions (Weimerskirch *et al.* 2010).

Imperial Cormorants (*Phalacrocorax atriceps*) are coastal foragers (Schreiber and Clapp 1987) distributed throughout the southern Atlantic and Pacific coast of Argentina and Chile (Murphy 1936). In Patago-

nia, Argentina, where colonies contain up to 6,000 pairs in more than 57 locations (Frere *et al.* 2005), birds feed mainly on benthic and in some cases pelagic prey (Malacalza *et al.* 1994; González Miri and Malacalza 1999; Bulgarella *et al.* 2008; Yorio *et al.* 2010) by dive pursuit (Wilson and Quintana 2004; Quintana *et al.* 2007). During the breeding season, males and females alternate <30 km daily foraging trips with caring for offspring at the nest (Quintana *et al.* 2011). Imperial Cormorants present sexual dimorphism (Svagej and Quintana 2007) that could reflect different physiological (Wilson *et al.* 2006) and, consequently, behavioral constraints to foraging (Quintana *et al.* 2011).

The objective of this research was to analyze the movements of adult breeding Imperial Cormorants while searching for food at-sea to determine the existence of different types of search behaviors. The specific objectives were to: i) determine if individuals performed Area-Restricted Search (ARS) and, if so, whether a nested ARS strategy occurred; ii) characterize the identified ARS areas, and iii) determine if different search behaviors could be detected based on the various characteristics of foraging paths and search scales used.

METHODS

Study Site

Field-work was conducted during the breeding seasons (November) of 2004, 2005, 2007 and 2008, at Punta León colony (43°04'S; 64°2'W). Imperial Cormorants (N = 3,894 pairs, Quintana *et al.* 2011) breed alongside Kelp Gulls (*Larus dominicanus*), two species of terns (*Thalasseus maximus* and *Thalasseus sandvicensis eurynatha*) and other marine birds (Yorio *et al.* 1994) in a mixed species assembly.

Forty-six breeding Imperial Cormorants (five males and seven females in 2004, six males and eight females in 2005, three males and five females in 2007, and four males and eight females in 2008) were caught at their nest prior to a foraging trip and equipped with GPS loggers (95 × 48 × 24 mm; weight <75g) (GPSlog, Earth and Ocean Technologies, Kiel, Germany) attached to their lower back feathers using waterproof tape (Wilson *et al.* 1997). Research was carried out in the Punta León provincial protected area under the project "Ecología pelágica de aves marinas buceadoras: determinación de movimientos y comportamiento en el mar mediante la utilización de registradores electrónicos de alta reso-

lución" directed by F. Quintana and authorized by the Province of Chubut (permit 2004/2005: Disp. N°19/04-DGCAP, Aut. N°13/04-DFyFS; 2006/2007: Disp. N°38/06-DGCAP, Aut. N°17/06-DFyFS; 2008/2009: Disp. N°13/08-DGCAP, Aut. N°31/08-DFyFS). Loggers were programmed to gather information on location (error \pm 5 m) in continuous mode (one fix per second) lasting the duration of one foraging trip (< 12 h). Based on this information it was possible to differentiate moments when the bird was: traveling (speed > 9 km/h with no signal interruptions); floating (speed < 8 km/h) and diving (fix acquisition was interrupted as the animal submerged) according to Quintana *et al.* (2011). Dive duration was estimated by the interval of time the GPS did not record during each presumed dive (see Quintana *et al.* 2011 for details). When more than one trip was performed and recorded within the day, only the first was used. If the beginning of the first trip was not complete because individuals left the colony before devices began recording, the second trip was analyzed instead. Maximum distance reached was measured from the furthest location recorded to the initial position (the nest), and trip duration was determined from the moment the individual began moving until it returned to the colony.

Existence of Area-Restricted Search (ARS) was evaluated for each trip. GPS positions were converted from geographic to UTM and transformed using a uniform distance interval of 5 m, to ensure points were equally represented (equivalent to Hamer *et al.* 2009, at a smaller scale). First-passage time analysis (fpt) was then performed using *adehabitat* and *ade4* packages in R 2.9.1. The time necessary to pass through a circle of a given diameter throughout the trajectory was determined for circles of increasing size at two scales: large = [0-10 km] every 100 m (error of estimation: 0.1 km), and small = [0-0.1 km] every 10 m (error of estimation: 0.01 km). By plotting the variance in first-passage time as a function of circle size, peaks of maximum variance were identified. The size of the circle corresponding to these peaks is the search scale (Fauchald and Tveraa 2003). Finally, first-passage time (for each search scale) was plotted against time elapsed and intervals of ARS were identified. To be more conservative in our detection of ARS areas and avoid false positives by individuals retracing their tracks as they returned to the colony, only intervals of passage time within the upper third of the passage time detected for the whole trip were included.

Tracks were visualized using a geographical information system program (ArcInfo 9.3 ESRI). ARS areas were defined as the smallest circles that included all the locations of increased passage time (following Hamer 2009). The resolution used for estimating ARS areas was that of the minimum radius at large (0.1 km²) and small (0.001 km²) scales. If more than one search scale was identified for one individual, the existence of one intensively searched area nested within a larger scale ARS was explored. The number and duration of dives before and during ARS areas were calculated and each of the latter was characterized by its size, geographical location and distance to the colony. Average bathym-

etry within each ARS area was extracted from a grid of 1.852 km resolution (GEBCO 2003) and the number and duration of dives before and during ARS were calculated. If more than one ARS area was identified for one individual, the largest ARS area was selected to determine the search scale used. Distance from the colony to the ARS area, proportion of dives before, during and after, as well as distance between the last dive prior to entering the ARS area and the ARS area itself, was determined. The correlation coefficient was estimated between search scale used and the following parameters: ARS area size, depth and distance from the colony, number of dives and dive duration within ARS, percentage of dives before and during Area-Restricted Search. The relationship between maximum distance reached and distance to ARS area as well as between depth and dive duration was also examined.

Other parameters calculated for each trip included percentage of time flying and diving, global straightness index (D/L) given by the maximum distance divided by the total distance covered (Benhamou 2004), total area/maximum distance (calculated as the area enclosed by the path divided by the maximum distance reached), landing rate calculated as the number of times the individual slowed down to < 8 km/h (floating) divided by the trip duration and distance from the colony to the first dive (distances under 1 km from the colony were discarded as individuals often landed on the water close inshore to cleanse before heading off to forage). Cluster analysis was performed on standardized variables: trip duration, maximum distance, (D/L), percentage of time flying, percentage of time diving, average dive duration, total area/ maximum distance, distance from the colony to first dive and number of landings per hour to select variables with less than 50% similarity and eliminate redundancy produced by highly correlated indicators. A cluster analysis of the tracks was then performed using the selected variables. The resulting groups of tracks (with a 50% similarity cut off level) were described based on common characteristics and search scales. Within each group, individuals without ARS were excluded from the calculation of average search scale, percentage of dives within ARS and distance from the last dive prior to entering the ARS and the ARS area.

General Linear Models were constructed to determine the effect of sex, year and their interaction on the depth of the ARS areas. The effect of sex (Mann-Whitney) and year (Kruskal-Wallis) were evaluated on the following parameters: maximum distance, trip duration, search scale, distance to ARS area, distance between the previous dive to and the ARS area itself, percentage of dives before and during ARS, as well as depth of ARS areas. Correlations between parameters were determined using the Spearman rank correlation test. Analyses were performed using STATISTICA 7.0 (significance set at $P < 0.05$). Cluster analysis was performed using the complete linkage method of the Squared Pearson Distance measure (cut off level of 50% similarity) in MINITAB 13.3. In all cases means were given \pm SD.

RESULTS

Foraging trips of 18 male and 28 female Imperial Cormorants instrumented in 2004, 2005, 2007 or 2008 were recorded. Daily trips were performed in an easterly to south-westerly direction from the colony, reaching a maximum distance of 28 ± 11 km from the colony, with no differences being detected between gender or year (Mann-Whitney U test, $z_{1,45} = -0.43$, $P = 0.67$ and Kruskal-Wallis $H_{3,45} = 3.38$, $P = 0.34$). On average, trip duration was longer for females than for males (6.3 ± 1.9 h vs. 5.3 ± 1.6 h) (Mann-Whitney U test $z_{1,45} = 2.23$, $P = 0.026$).

Area-Restricted Search Areas

Area-Restricted Search (ARS) zones, detected by first-passage time, were identified for 43 of the 46 individuals analyzed (see example in Fig. 1). ARS scales ranged from 0.03 ± 0.01 km to 6.0 ± 0.1 km (average: 1.7 ± 1.5 km), with individuals using one, two or three search scales during a single foraging trip. The resulting ARS areas, for a given scale, differed in size and time spent within them (approximately 3 km^2 and 2 h in the example in Fig. 1). ARS areas ranged from 0.01 km^2 to 33.0 km^2 and individuals spent between 2 and 326 min within them. Search

scale size, distance from the colony to the ARS area and from the last dive prior to and the given ARS area, as well as the percentage of dives performed before and during Area-Restricted Search did not differ significantly between sexes and years (Table 1). A total of 84 areas were identified for these 43 individuals, as some individuals searched intensively in up to three distinct locations.

Nested ARS

A nested search strategy was detected in 22 (13 males and nine females) of the 43 individuals that performed ARS (four of eleven in 2004, eight of twelve in 2005, five of eight in 2007 and five of twelve in 2008, Fig. 2). During these trips, at least two ARS areas were identified, with the smaller scale area (average scale 0.4 ± 0.5 km, $N = 27$) located within the larger area (average scale 2.7 ± 1.7 km, $N = 23$). Individuals without nested ARS presented intermediate search scales (average scale 0.9 ± 1.1 km, $N = 34$).

ARS Scales

For the 84 identified ARS areas, search scales were positively correlated to ARS area size (Spearman rank correlation $r_s = 0.84$, $P < 0.005$), though not to the bathymetric depth of the given area ($r_s = 0.03$, $P = 0.84$). Search scales were also positively correlated to the number of dives performed within these areas ($r_s = 0.53$, $P < 0.005$) but not to their duration ($r_s = -0.17$, $P = 0.12$) (Table 2).

Within each trip evidencing Area-Restricted Search ($N = 43$), distance to the largest ARS area was highly correlated to maximum distance reached ($r_s = 0.99$, $P < 0.01$) and ARS areas were located at the maximum distance in 72% of these trips. However, distance to a given ARS area was not correlated to the magnitude of its search scale (Spearman rank correlation $r_s = 0.26$, $P = 0.10$). Search scale used in each case was negatively correlated to the percentage of dives performed before and positively correlated to the percentage of dives during ARS ($r_s = -0.41$, $P = 0.006$ before and $r_s = 0.59$, $P < 0.005$ during ARS).

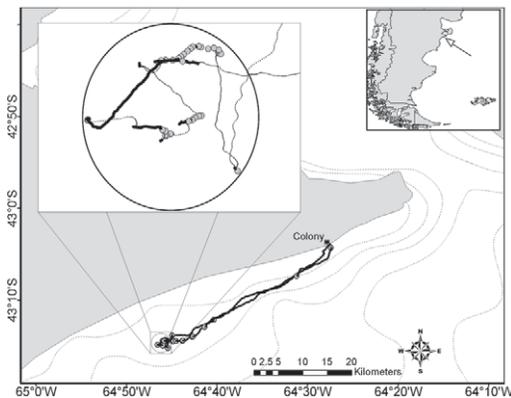


Figure 1. Foraging track of a male Imperial Cormorant (*Phalacrocorax atriceps*) from Punta León in 2008 breeding season. Dotted lines indicate flight, thicker lines indicate floating and grey circles indicate dives. ARS area enclosed by hollow circle. 15 meter isobaths indicated with dotted lines.

Table 1. Characteristics of the foraging paths of 43 Imperial Cormorants (*Phalacrocorax atriceps*) breeding at Punta León that presented Area-Restricted Search. Comparisons between gender (17 males and 26 females, Mann-Whitney U test) and years (2004, 2005, 2007 and 2008, Kruskal-Wallis test), $z_{1,42}$, $H_{3,42}$ and P-values are given, significance at $P < 0.05$.

Variable	mean \pm SD	gender	year
Search scale (km)	1.7 \pm 1.5	$z_{1,42} = -0.87$ P = 0.87	$H_{3,42} = 3.14$ P = 0.37
Distance to ARS area (km)	27 \pm 11	$z_{1,42} = -0.12$ P = 0.90	$H_{3,42} = 4.09$ P = 0.25
Distance between last dive previous to and ARS area (km)	4 \pm 5	$z_{1,42} = -0.12$ P = 0.90	$H_{3,42} = 2.88$ P = 0.41
% dives before ARS	27 \pm 17	$z_{1,42} = 0.41$ P = 0.68	$H_{3,42} = 1.21$ P = 0.75
% dives during ARS	51 \pm 29	$z_{1,42} = -1.17$ P = 0.24	$H_{3,42} = 0.91$ P = 0.82

Depth of ARS areas ranged between 1 and 60 m, and dive duration within these areas was significantly correlated to depth (Spearman rank correlation $r_s = -0.40$, $P < 0.005$, $N = 84$). Average depth did not vary between sexes or years alone, but there was a

significant effect of the interaction between sex and year (GLM with sex $F_{1,38} = 3.64$, $P = 0.06$, year $F_{3,38} = 1.03$, $P = 0.389$ and sex \times year $F_{3,38} = 3.20$, $P = 0.034$). In 2004, average depth of ARS areas was 28 ± 16 m, with no differences detected between sexes (Mann-Whitney $z_{1,11} = 1.70$, $P = 0.09$), though most females searched intensively within the 30 to 45 m depth range. In 2005, males dived in waters of an average depth of 36 ± 21 m and females of 8 ± 6 m (Mann-Whitney $z_{1,12} = 2.24$, $P = 0.02$). In 2007, average depth of these areas was 34 ± 9 m, with no significant differences occurring between genders (Mann-Whitney $z_{1,8} = 0.596$, $P = 0.55$), though most females searched intensively in the 45 to 60 m depth range. And in 2008, the average depth of ARS areas was 28 ± 16 m, with no differences between gender (Mann-Whitney $z_{1,12} = 0.17$, $P = 0.87$). In general, females seemed to use a narrower depth range within each year than males. The location of ARS areas also varied amongst years (Fig. 2).

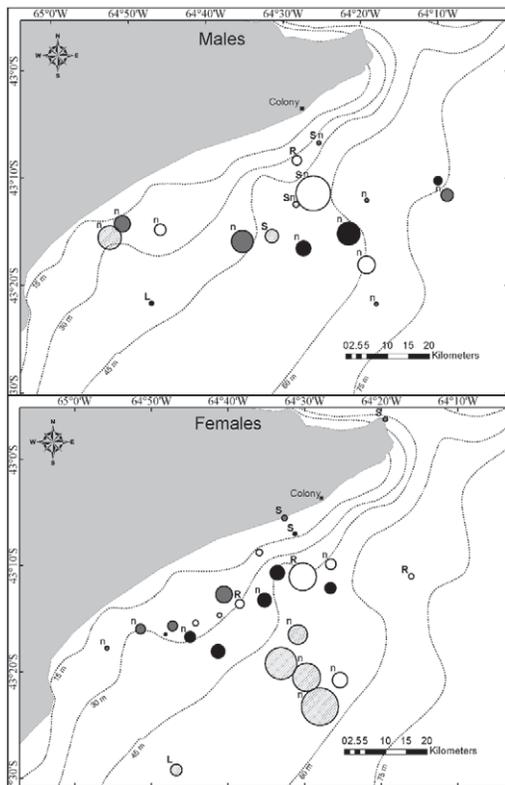


Figure 2. ARS areas of 43 Imperial Cormorants (*Phalacrocorax atriceps*) symbolized by circles (year 2004 filled in black, 2005 in dark grey, 2007 thatched and 2008 in white). Males ($N = 18$) in the upper panel and females ($N = 26$) in the lower panel. Trips classified as: S: short direct return trips; L: loops; R: random flight searches, the rest were long direct return trips. Nested ARS indicated with n. 15 meter isobaths indicated with dotted lines.

Search Behaviors

Following a cluster analysis, seven variables with low correlation between them were selected (Fig. 3). A new cluster analysis of the tracks using these variables with a 50% similarity cut off level revealed four search behaviors (Fig. 4 and Table 3, indicated with letters in Fig. 2). Based on search scale and foraging path characteristics, foraging tracks were classified as follows:

Cluster 1: Short direct return trips. Four males and three females (15% of studied birds) belonged to this group. For one male and two females this was their second trip within that day. Individuals trav-

Table 2. Characteristics of all identified search scales (N = 84), of the 43 Imperial Cormorants (*Phalacrocorax atriceps*) that presented ARS, grouped into categories. m: male, f: female. Number of individuals indicated between brackets. * search scales calculated using a radius size error of 0.01 km; for the rest of the scales, error of 0.1 km.

ARS scale (km)	Gender	Year	ARS area (km ²)	time in ARS (min)	n dives in ARS	Dive duration ARS (min)	Depth ARS area (m)
0 - 0.10*	m (9)	2004 (4)	0.15 ± 0.21	29 ± 33	8 ± 10	2 ± 1	30 ± 18
		2005 (6)					
	2007 (2)						
	2008 (6)						
0.1 - 0.5	m (4)	2004 (1)	1.3 ± 1.8	72 ± 35	24 ± 22	2 ± 1	32 ± 15
	f (11)	2005 (6)					
		2007 (3)					
0.5 - 1	m (8)	2004 (4)	1.1 ± 1.5	90 ± 38	31 ± 23	1 ± 1	21 ± 16
		2005 (11)					
	f (13)	2007 (2)					
1 - 2.5	m (9)	2004 (7)	4.6 ± 4.6	123 ± 77	35 ± 36	2 ± 1	34 ± 15
		2005 (1)					
	f (8)	2007 (5)					
> 2.5	m (6)	2004 (2)	10.8 ± 8.5	165 ± 90	34 ± 14	2 ± 1	27 ± 14
		2005 (6)					
	2007 (3)						
	f (7)	2008 (2)					

eled short distances to a given feeding area (short maximum distance) (Table 3), where they performed approximately 28 ± 19 dives per hour at an average depth of 19 ± 19 m. Trips were characterized by short total duration in which a high percentage of time was spent diving. Search scales covered a large range (0.03 km to 2.9 km),

though more than 57% of search scales were smaller than 0.5 km (Fig. 5a and Table 3).

Cluster 2: Long direct return trips. Eleven males and 20 females (68% of studied birds)

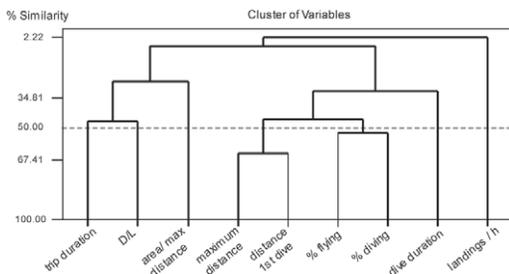


Figure 3. Cluster analysis of the variables: trip duration, maximum distance, global straightness index (D/L), % time flying, % time diving, average dive duration, total area/maximum distance, distance to 1st dive and landings per hour using the complete linkage method to evaluate the absolute correlation between them. Using a 50% similarity cut off level, seven variables are selected: trip duration, maximum distance, D/L, % diving, average dive duration, total area/maximum distance and landings per hour.



Figure 4. Cluster analysis of 46 tracks of Imperial Cormorants (*Phalacrocorax atriceps*) using complete method of the Square Pearson distance measure on the standardized variables: trip duration, maximum distance, D/L, % time diving, average dive duration, total area/maximum distance and number of landings per hour. Using 50% similarity cut off level, four clusters are separated: 1: four males (2005, 2007 and 2008), three females (2004 and 2005); 2: eleven males (2004, 2005, 2007 and 2008), 20 females (2004, 2005, 2007 and 2008); 3: two males (2004 and 2008), four females (2005 and 2008); 4: one male (2004), one female (2007). Males: m, females: f. Symbols for sex and year indicated in inset. Individuals without detectable ARS indicated with *.

Table 3. Foraging trip characteristics for each of the four search behaviors Imperial Cormorants (*Phalacrocorax atriceps*) presented in seasons 2004, 2005, 2007 and 2008, identified by cluster analysis. m: male, f: female. Number of individuals indicated between brackets.

	Cluster 1	Cluster 2	Cluster 3	Cluster 4
Description	<i>short direct return trip</i>	<i>long direct return trip</i>	<i>random flight search</i>	<i>Loop-shaped trip</i>
Sex	m (4) 22% f (3) 11%	m (11) 61% f (20) 71% ^a	m (2) 11% ^a f (4) 14% ^a	m (1) 6% f (1) 4%
Year	2004 (1) 8.3% 2005 (3) 21.4% 2007 (2) 25% 2008 (1) 8.3%	2004 (9) 75% 2005 (10) 71.4% ^a 2007 (5) 62.5% 2008 (7) 58.3%	2004 (1) 8.3% ^a 2005 (1) 7.1% ^a 2007 0% 2008 (4) 33.3%	2004 (1) 8.3% 2005 0% 2007 (1) 12.5% 2008 0%
Trip duration (h)	3.6 ± 1.7	5.9 ± 1.2	7.9 ± 2.0	8.3 ± 0.4
Mode scale range (km)	[0.1-0.5]	[1-2.5]	[0-0.1]	[0.1-0.5]
Search scale average (km)	0.9 ± 1.1	2.1 ± 1.5	0.4 ± 0.3	0.4 ± 0.1
n with nested ARS/total	3 / 7	19 / 31	0 / 6	0 / 2
Maximum distance (km)	15 ± 5	29 ± 9	26 ± 8	52 ± 3
% flying	26 ± 15	24 ± 14	20 ± 11	46 ± 28
% diving	41 ± 15	30 ± 8	24 ± 11	16 ± 9
% floating	33 ± 8	47 ± 11	56 ± 15	38 ± 19
Total n dives	142 ± 107	77 ± 42	114 ± 34	135 ± 14
% dives ARS	44 ± 35	57 ± 25	27 ± 44	18 ± 12
Average dive duration (min)	1.2 ± 0.7	1.6 ± 0.6	1.0 ± 0.5	0.6 ± 0.3
Distance previous dive to ARS (km)	2. ± 2	4 ± 6	4 ± 4	3 ± 1
Landings per hour	3 ± 1	2 ± 1	3 ± 1	2 ± 1

^aincludes one individual without detectable ARS.

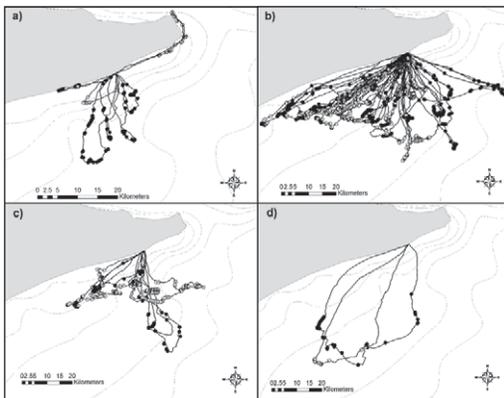


Figure 5. a) Foraging tracks of Imperial Cormorants (*Phalacrocorax atriceps*) classified in each type of behavior: Cluster 1: Short direct return trips; b) Cluster 2: Long direct return trips; c) Cluster 3: Random flight searches; d) Cluster 4: Loop-shaped trips. Male dives are indicated with (●) and female dives are indicated with (○).

belonged to this group. Individuals traveled further away from the colony to a given ARS area, usually located at the furthest point of their trajectory (time spent within ARS area: 2.5 ± 1.5 h). Relatively few long dives were made. The highest percentage of dives took place within ARS areas, with few dives

occurring before and after. This group presented the largest average search scale and most individuals (19 of 30) presented more than one search scale, in some cases with the smaller area (scale 0.4 ± 0.5 km, $N = 24$) nested within a larger one (scale 2.5 ± 1.6 km, $N = 20$) (Table 3). Isolated dives during the outgoing phase of the trip were interspaced with relatively straight flight paths and orientation towards the ARS areas was not significantly modified in flight thereafter. Search scales covered a large range, though 32% of the trips had search scales within the 1 to 2.5 km range (Fig. 5b and Table 3).

Cluster 3: Random flight search. Two males and four females (13% of studied birds) were classified as belonging to this type. Foraging paths presented the highest tortuosity (lowest D/L) and lowest average ARS scale size (two individuals with no detectable ARS belong to this group). Individuals spent a higher percentage of time floating than others and performed a large amount of dives, but a relatively low proportion within ARS areas. Fifty percent of this kind of trip had search scales smaller than 0.1 km and the largest was 0.7 km (Fig. 5c and Table 3).

Cluster 4: Loop-shaped trips. One male and one female (4% of studied birds) belonged to this group. Trajectories covered the largest total area relative to maximum distance reached and individuals traveled furthest from the colony (Table 3). They spent most of their time in flight and a low percentage diving. Search scales were maintained within the 0.1 to 0.5 km range. Landing rate was the lowest and trip duration was the longest (average: 8.3 ± 0.4 h). Average dive duration throughout was the shortest (Fig. 5d and Table 3).

DISCUSSION

Forty-three of 46 Imperial Cormorants studied in the Punta León colony performed Area-Restricted Search, searching at fine to coarse scales. Most intensively searched areas were at the furthest distance reached from the colony and 22 individuals (47%) searched at two scales, with the smaller nested within a larger area. Search scales were related to size of ARS areas as well as number of dives before and within these areas, linking search behavior to dive occurrence. However, search scales were not related to location of ARS areas, and year and sex did not have a significant effect on the search scales used. Four search behaviors were separated by analysis based on various characteristics of the foraging paths and search scales detected: short direct return trips, long direct return trips, random flight searches and loop-shaped trips. Males and females presented the four kinds of behavior and no significant differences were detected between years.

Individuals with ARS increased the amount of time invested in a certain area at some point during their foraging trip, and dived at least twice within it. Given the effort required for prey acquisition in this species (Shepard *et al.* 2009), an increase in time and dive occurrence may be necessary for cormorants to obtain prey whereby an absence of ARS could be indicative of individuals being unsuccessful at acquiring prey. Of the three individuals that did not exhibit ARS behavior, two did random flight searches, a male in 2004 and a female

in 2005, and one female did a long direct return trip in 2005. In these cases, the particular prey type being targeted may have been depleted or have moved from the location where individuals were searching. All remaining trips included ARS, independently from the search behavior individuals displayed, and search scales were linked to how, but not where, individuals foraged.

If orientation towards prey is based on perception of environmental cues or by detecting prey patches directly, the search scale used will be defined by the individual's perceptual range (Olden *et al.* 2004). As cormorants depend, at least partly, on vision to detect prey the maximum range individuals are able to cover at each location will be determined, to some extent, by the visual range they can achieve both above and under water linked to the prey type consumed (Elliott *et al.* 2009). Below the surface, other mechanisms as well as vision (White *et al.* 2007) may be used to search for prey on vertical and horizontal planes as some prey species may have cryptic coloration and/or hide in the seafloor substrate. The use of more than one search scale nested within a larger one may indicate a higher level of complexity in foraging behavior, which would be advantageous at this colony during the spring-summer when the Sistema Frontal Nordpatagónico is present and generates a stable nutrient-rich environment for prey (Acha *et al.* 2004; Rivas 2006).

Search scales reflect the predators' orientation mechanisms as well as the type and distribution of prey (Fauchald *et al.* 2000; Pinaud and Weimerskirch 2007; Mueller and Fagan 2008). If prey is distributed in abundant, stable patches and predators can track the system effectively, then the memory component of their behavior may become stronger (Cook *et al.* 2005; Fauchald and Tveraa 2006). In this case, the extent of tuning to a specific prey location will depend on previous foraging success (Fauchald 2009). Long and short direct return trips, consisting of straight flight paths to and from the feeding area, would emerge from a combination of perceptual and memory-based mechanisms. Individuals grouped here presented a range

of small to large search scales (up to 6 km) and were the most common across all years. Consistent with these results, the most common prey consumed by Imperial Cormorants during the breeding season (according to Malacalza *et al.* 1994) are demersal fish species *Raneya fluminensis* and *Triathalassothia argentina* and to a lesser extent the more inshore benthic species *Ribeiroclinus eigenmanni* and *Agonopsis chilensis*. As targeted prey are associated with the sea floor to a certain degree, due to their feeding and/or reproductive habits (FishBase 2011), birds could be searching at larger scales for substrates or depths where prey presence is more likely.

If individuals do not use any mechanism to orientate towards prey, the most effective way of coming across randomly distributed prey patches is with an almost straight trajectory (Zollner and Lima 1999) as occurs in loop-shaped trips (Benhamou 2004; Pinaud and Weimerskirch 2007; Zavalaga *et al.* 2010). Trips identified as loops in this study showed smaller search scales than long direct return trips, even though birds traveled further from the colony. In this case, individuals could be searching for a particular prey without having any information on its current location, either because prey is spatio-temporally unpredictable or because the individual has not tapped into a prey source that may be stable. Some individuals from this colony feed on hake (*Merluccius hubbsi*), an offshore pelagic fish that migrates closer to shore to spawn in summer (Pájaro *et al.* 2005) coming within range of individuals that will try to cover the largest area and go as far as possible on an initial trip to maximize probability of an encounter.

Search scales that depend on perceptual traits could also be reduced by local enhancement, either by conspecifics or other species feeding on target prey (Davoren *et al.* 2003; Weimerskirch *et al.* 2010). Visualization of other birds flying to or from feeding areas could improve detection of prey and therefore reduce the search scale used. Consistent with these assumptions, individuals with random flight searches presented small or even non-existent search scales, an effective opportunistic behav-

ior especially when foraging close to the colony. Anchovy, *Engraulis anchoita*, is a pelagic schooling fish that migrates south into the region surrounding the colony of Punta León in November (Pájaro 2002) and becomes an important item in the diet of cormorants at this time (Malacalza *et al.* 1994). Given the mobility of schooling anchovy, multispecies aggregations may form at these locations and individuals could then join these feeding groups.

Foraging is a costly activity for the individual (Wilson *et al.* 2006) and therefore optimization of at least one behavioral trait is expected to occur (Charnov 1976; Perry and Pianka 1997). During long direct return trips, individuals could be maximizing gross energy intake (Shepard *et al.* 2009) by consuming either more or higher quality prey (González Miri and Malacalza 1999) further away from the colony with the consequent increase in time and/or energy investment. Individuals with short direct return trips had the lowest journey duration and area covered, minimizing time invested in the trip. Short foraging trips would be advantageous when prey is abundant close to the colony, but individuals may be subject to intra- and even interspecific competition and, in the long term, depletion of resources close by (Ashmole 1963; Gaston *et al.* 2007). In some cases, individuals performed two trips within a day in which second trips were consistently short direct return trips where time would be the limiting factor for food searching. Individuals could be feeding on readily accessible polychaete and molluscs or even crustaceans and small fish. Random flight searches would be expected if prey were unpredictable in space and/or time or if individuals are not able to track the system effectively, in which case the behavior of conspecific or other species may become important. Loops would be developed as an effective way of maximizing the area covered by individuals with little or no information on location of prey patches.

ARS scale size has been related to species and oceanographic characteristics in large-scale foragers such as albatrosses and petrels (Fritz *et al.* 2003; Suryan *et al.* 2006;

Pinaud and Weimerskirch 2007). Within a population of a given species, different search strategies have been identified, such as “sit-and-wait” and “foraging in flight” in Yellow-nosed Albatross (*Thalassarche chlororhynchos*), short and long foraging trips in Antarctic Petrels (*Thalassoica antarctica*) and Cory’s Shearwaters (*Calonectris diomedea*), or the presence of “direct return” and “loop-shaped trips” in Guanay Cormorants (*Phalacrocorax bougainvilli*) and Peruvian Boobies (*Sula variegata*) (Pinaud and Weimerskirch 2005; Fauchald and Tveraa 2006; Weimerskirch *et al.* 2007, 2010; Zavalaga *et al.* 2010; Paiva *et al.* 2010; Quintana *et al.* 2011). The coexistence of several search strategies within a population can produce a stabilizing effect on the oceanic environment used, reducing intraspecific competition, either by diversifying behavior while searching for similar prey or by targeting different prey types. Predators adjust their behavior to the current prey system and the bigger the area available for predator-prey interaction, the larger the stabilizing effect given by these behavioral adjustments (Fauchald 2009; Weimerskirch *et al.* 2010). The four behavioral types identified in this study occurred in more than one breeding season, reinforcing the idea that behavioral variability in foraging strategies is present in this population. No significant differences were detected between sexes for all years taken together, though females seemed to use narrower depth ranges than males during each breeding season. Further research is needed to determine if behavioral differences are related to prey type (Tremblay *et al.* 2005; Garthe *et al.* 2006; Elliott *et al.* 2008) and distribution (Fauchald *et al.* 2000; Garthe *et al.* 2007; Hamer *et al.* 2009), reproductive stage or individual characteristics, such as experience (Cook *et al.* 2005; Daunt *et al.* 2007; Weimerskirch *et al.* 2010) and body condition (Woo *et al.* 2008) and to infer the level of foraging plasticity required when faced with environmental change caused by seasonal migrations of prey (Pájaro 2002) or longer-term modifications in the South-western Atlantic Ocean that these and other seabirds exploit (Boersma 2008).

ACKNOWLEDGMENTS

Research was funded by grants from the Consejo Nacional de Investigaciones Científicas y Técnicas de la República Argentina and Wildlife Conservation Society, and Agencia de Promoción Científica y Tecnológica to F. Quintana. We thank the Organismo Provincial de Turismo of the Province of Chubut for permits to work at Punta León, the Centro Nacional Patagónico (CENPAT-CONICET) and Centro Austral de Investigaciones Científicas (CADIC-CONICET) for institutional support, and R. Wilson, M. Uhart, W. Svagelj, E. Shepard and A. Gómez Laich for assistance in various aspects of this research. S. Harris was supported by a Ph.D. fellowship from CONICET.

LITERATURE CITED

- Acha, E. M., H. W. Mianzan, R. A. Guerrero, M. Favero and J. Bava. 2004. Marine fronts at the continental shelves of austral South America - Physical and ecological processes. *Journal of Marine Systems* 44: 83-105.
- Angelier, F., S. A. Shaffer, H. Weimerskirch, C. Trouvé and O. Chastel. 2007. Corticosterone and foraging behaviour in a pelagic seabird. *Physiological and Biochemical Zoology* 80: 283-292.
- Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103: 458-473.
- Benhamou, S. 2004. How to reliably estimate the tortuosity of an animal's path: Straightness, sinuosity, or fractal dimension? *Journal of Theoretical Biology* 229: 209-220.
- Boersma, P. D. 2008. Penguins as Marine Sentinels. *BioScience* 58: 597-607.
- Bulgarella, M., L. C. Pizzarro, F. Quintana, A. Sapozhnikov, A. Gosztonyi and L. Kuba. 2008. Diet of Imperial Cormorants (*Phalacrocorax atriceps*) and Rock Shags (*P. magellanicus*) breeding sympatrically in Patagonia, Argentina. *Ornitología Neotropical* 19: 553-563.
- Cook, T. R., Y. Cherel and Y. Tremblay. 2005. Foraging tactics of chick-rearing Crozet shags: Individuals display repetitive activity and diving patterns over time. *Polar Biology* 29: 562-569.
- Charnov, E. L. 1976. Optimal foraging: The marginal value theorem. *Theoretical Population Biology* 9: 129-136.
- Daunt, F., S. Wanless, M. P. Harris, L. Money and P. Monaghan. 2007. Older and wiser: Improvements in breeding success are linked to better foraging performance in European shags. *Functional Ecology* 21: 561-567.
- Davoren, G. K., W. A. Montevecchi and J. T. Anderson. 2003. Distributional patterns of a marine bird and its prey: Habitat selection based on prey and conspecific behaviour. *Marine Ecology Progress Series* 256: 229-242.
- Elliott, K. H., K. Woo, A. J. Gaston, S. Benvenuti, L. Dall'Antonia and G. K. Davoren. 2008. Seabird for-

- aging behaviour indicates prey type. *Marine Ecology Progress Series* 354: 289-303.
- Elliott, K. H., R. D. Bull, A. J. Gaston and G. K. Davoren. 2009. Underwater and above-water search patterns of an Arctic seabird: Reduced searching at small spatiotemporal scales. *Behavioral Ecology and Sociobiology* DOI 10.1007/s00265-009-0801-y
- Fauchald, P. 2009. Spatial interaction between seabirds and prey: Review and synthesis. *Marine Ecology Progress Series* 391: 139-151.
- Fauchald, P., K. E. Erikstad and H. Skarsfjord. 2000. Scale-dependent predator-prey interactions: The hierarchical spatial distribution of seabirds and prey. *Ecology* 81: 773-783.
- Fauchald, P. and T. Tveraa. 2003. Using First-Passage Time in the analysis of Area-Restricted Search and habitat selection. *Ecology* 84: 282-288.
- Fauchald, P. and T. Tveraa. 2006. Hierarchical patch dynamics and animal movement pattern. *Oecologia* 149: 383-395.
- Fernández, M., D. Hernández and A. Roux. 2007. Distribución espacial del langostino patagónico (*Pleoticus muelleri*, (Bate, 1888)) y su relación con las variables ambientales, Golfo San Jorge, Argentina. *Revista de Biología Marina y Oceanografía* 42 : 335-344.
- FishBase. 2011. Data from FishBase Database. <http://www.fishbase.org/search.php>, accessed 28 October 2011.
- Frere, E., F. Quintana and P. Gandini. 2005. Cormoranes de la costa patagónica: Estado poblacional, ecología y conservación. *El Hornero* 20: 35-52.
- Fritz, H., S. Said and H. Weimerskirch. 2003. Scale-dependent hierarchical adjustments of movement patterns in a long-range foraging seabird. *Proceedings of the Royal Society of London Series B Biological Sciences* 270: 1143-1148.
- Garthe, S., W. A. Montevecchi, G. Chapdelaine, J. F. Rail and A. Hedd. 2006. Contrasting foraging tactics by Northern Gannets (*Sula bassana*) breeding in different oceanographic domains with different prey fields. *Marine Biology* 151: 687-694.
- Garthe, S., W. A. Montevecchi and G. K. Davoren. 2007. Flight destinations and foraging behaviour of Northern Gannets (*Sulla bassana*) preying on a small forage fish in a low-Arctic ecosystem. *Deep-Sea Research Part II* 54: 311-320.
- Gaston, A. J., R. C. Ydenberg and G. E. J. Smith. 2007. Ashmole's halo and population regulation in seabirds. *Marine Ornithology* 35: 119-126.
- González Miri, L. and V. Malacalza. 1999. Perfil nutricional de las principales especies en la dieta del Cormorán Real (*Phalacrocorax albiventer*) en Punta León (Chubut, Argentina). *Ornitología Neotropical* 10: 55-59.
- Hamer, K. C., E. M. Humphreys, M. C. Magalhães, S. Garthe, J. Henricke, G. Peters, D. Grémillet, H. Skov and S. Wanless. 2009. Fine-scale foraging behaviour of a medium-ranging marine predator. *Journal of Animal Ecology* 78: 880-889.
- Hawkes, C. 2009. Linking movement behaviour, dispersal and population processes: is individual variation a key? *Journal of Animal Ecology* 78: 894-906.
- Kareiva, P. M. and N. Shigesada. 1983. Analyzing insect movement as a correlated random walk. *Oecologia* 56: 234-238.
- Kareiva, P. and G. Odell. 1987. Swarms of predators exhibit "preytaxis" if individual predators use Area-Restricted Search. *American Naturalist* 130: 233-270.
- Lewis, S., S. Benvenuti, L. Dall'Antonia, R. Griffiths, L. Money, T. N. Sherratt, S. Wanless and K. C. Hamer. 2002. Sex-specific foraging behaviour in a monomorphic seabird. *Proceedings of the Royal Society of London Series B Biological Sciences* 269: 1687-1693.
- Malacalza, V. E., T. I. Poretti and N. M. Bertellotti. 1994. La dieta de *Phalacrocorax albiventer* en Punta León (Chubut, Argentina) durante la temporada reproductiva. *Ornitología Neotropical* 5: 91-97.
- Mueller, T. and W. F. Fagan. 2008. Search and navigation in dynamic environments - from individual behaviors to population distributions. *Oikos* 117: 654-664.
- Murphy, R. C. 1936. *Oceanic Birds of South America*. Vols. 1-2. The MacMillan Company. The American Museum of Natural History, New York.
- Nevitt, G. 1999. Olfactory foraging in Antarctic seabirds: A species-specific attraction to krill odors. *Marine Ecology Progress Series* 177: 235-241.
- Orians, G. H. and N. E. Pearson. 1979. On the theory of central place foraging. Pages 154-177 in *Analysis of Ecological Systems* (D. J. Horn, R. D. Mitchell and G. R. Stairs, Eds.). Ohio State University Press, Columbus.
- Olden, J. D., R. L. Schooley, J. B. Monroe and N. L. Poff. 2004. Context-dependent perceptual ranges and their relevance to animal movements in landscapes. *Journal of Animal Ecology* 73: 1190-1194.
- Paiva, V. H., P. Geraldés, I. Ramírez, S. Garthe and J. A. Ramos. 2010. How area restricted search of a pelagic seabird changes while performing a dual foraging strategy. *Oikos* 119: 1423-1434.
- Pájaro, M. 2002. Alimentación de la anchoíta argentina (*Engraulis anchoíta* Hubbs y Marini, 1935) (Pisces: Clupeiformes) durante la época reproductiva. *Revista de Investigación y Desarrollo Pesquero* 15: 111-125.
- Pájaro, M., G. J. Macchi and P. Martos. 2005. Reproductive pattern of the Patagonian stock of Argentine hake (*Merluccius hubbsi*). *Fisheries Research* 72: 97-108.
- Perry, G. and E. R. Pianka. 1997. Animal foraging: Past, present and future. *TREE* 12: 360-364.
- Pinaud, D. and H. Weimerskirch. 2005. Scale-dependent habitat use in a long-ranging central place predator. *Journal of Animal Ecology* 74: 852-863.
- Pinaud, D. and H. Weimerskirch. 2007. At-sea distribution and scale-dependent foraging behaviour of petrels and albatrosses: A comparative study. *Journal of Animal Ecology* 76: 9-19.
- Quillfeldt, P., S. Schroff, H. J. van Noordwijk, A. Michalik, K. Ludynia and J. F. Masello. 2011. Flexible foraging behavior of a sexually dimorphic seabird: Large males do not always dive deep. *Marine Ecology Progress Series* 428: 271-287.

- Quintana, F., R. P. Wilson and P. Yorio. 2007. Dive depth and plumage air in wettable birds: The extraordinary case of the Imperial Cormorant. *Marine Ecology Progress Series* 334: 299-310.
- Quintana, F., R. Wilson, P. Dell'Arciprete, E. Shepard and A. Gómez Laich. 2011. Women from Venus, men from Mars: Inter-sex foraging differences in the Imperial Cormorant *Phalacrocorax atriceps* a colonial seabird. *Oikos* 120: 350-358.
- R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rivas, A. L. 2006. Quantitative estimation of the influence of surface thermal fronts over chlorophyll concentration at the Patagonian Shelf. *Journal of Marine Systems* 63: 183-190.
- Schreiber, R. W. and R. B. Clapp. 1987. Pelecaniform feeding ecology. Pages 173-188 in *Seabirds: feeding ecology and role in marine ecosystems* (J. P. Croxall, Ed.). Cambridge University Press, Cambridge, UK.
- Shepard, E. L. C., R. P. Wilson, F. Quintana, A. Gómez Laich and D. W. Forman. 2009. Pushed for time or saving on fuel: Fine scale energy budgets shed light on currencies in a diving bird. *Proceedings of the Royal Society B Biological Sciences* 276: 3149-3155.
- Suryan, R. M., F. Sato, G. R. Balogh, K. D. Hyrenbach, P. R. Sievert and K. Ozaki. 2006. Foraging destinations and marine habitat use of Short-tailed Albatrosses: A multi-scale approach using first-passage time analysis. *Deep-Sea Research Part II* 53: 370-386.
- Svagej, W. and F. Quintana. 2007. Sexual size dimorphism and sex determination by morphometric measurements in breeding Imperial Shags (*Phalacrocorax atriceps*). *Waterbirds* 30: 97-102.
- Tremblay, Y., T. R. Cook and Y. Cherel. 2005. Time budget and diving behaviour of chick-rearing Crozet Shags. *Canadian Journal of Zoology* 83: 971-982.
- Weimerskirch, H., D. Pinaud, F. Pawlowski and C. A. Bost. 2007. Does prey capture induce Area-Restricted Search? A fine-scale study using GPS in a marine predator, the Wandering Albatross. *American Naturalist* 170: 734-743.
- Weimerskirch, H., S. A. Shaffer, Y. Tremblay, D. P. Costa, H. Gadenne, A. Kato, Y. Ropert-Coudert, K. Sato and D. Auriolles. 2009. Species- and sex-specific differences in foraging behaviour and foraging zones in Blue-footed and Brown Boobies in the Gulf of California. *Marine Ecology Progress Series* 391: 267-278.
- Weimerskirch, H., S. Bertrand, J. Silva, J. C. Marques and E. Goya. 2010. Use of social information in seabirds: Compass rafts indicate the heading of food patches. *PLoS ONE* 5(3): e9928. doi:10.1371/journal.pone.0009928.
- White, C. R., N. Day, P. J. Butler and G. R. Martin. 2007. Vision and foraging in cormorants: More like herons than hawks? *PLoS ONE* 2(7): e639. DOI: 10.1371/journal.pone.0000639.
- White, C. R., P. J. Butler, D. Grémillet and G. R. Martin. 2008. Behavioural strategies of cormorants Phalacrocoracidae foraging under challenging light conditions. *Ibis* 150: 231-239.
- Wilson, R. P., K. Pütz, G. Peters, B. Culik, J. A. Scolaro, J. B. Charrassin and Y. Ropert-Coudert. 1997. Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wildlife Society Bulletin* 25: 101-106.
- Wilson, R. P. and F. Quintana. 2004. Surface pauses in relation to dive duration in Imperial Cormorants; how much time for a breather? *Journal of Experimental Biology* 207: 1789-1796.
- Wilson, R. P., C. R. White, F. Quintana, L. G. Halsey, N. Liebsch, G. R. Martin and P. J. Butler. 2006. Moving toward acceleration for estimates of activity-specific metabolic rate in free-living animals: The case of the cormorant. *Journal of Animal Ecology* 75: 1081-1090.
- Woo, K. J., K. H. Elliott, M. Davidson, A. J. Gaston and G. K. Davoren. 2008. Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour. *Journal of Animal Ecology* 77: 1082-1091.
- Yorio, P., F. Quintana, C. Campagna and G. Harris. 1994. Diversidad, abundancia y dinámica espacio-temporal de la colonia mixta de aves marinas de Punta León, Patagonia. *Ornitología Neotropical* 5: 69-77.
- Yorio, P., S. Copello, L. Kuba, A. Gosztonyi and F. Quintana. 2010. Diet of Imperial Cormorants *Phalacrocorax atriceps* breeding at central Patagonia, Argentina. *Waterbirds* 33: 70-78.
- Zavalaga, C. B., J. N. Halls, G. P. Mori, S. A. Taylor and G. Dell'Omó. 2010. At-sea movement patterns and diving behavior of Peruvian Boobies *Sula variegata* in northern Peru. *Marine Ecology Progress Series* 404: 259-274.
- Zollner, P. A. and S. L. Lima. 1999. Search strategies for landscape-level interpatch movements. *Ecology* 80: 1019-1030.